Demography of a high-density coyote population

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Abstract: The demography of a lightly exploited population of coyotes (*Canis latrans*) in Webb County, Texas, which has had historically high densities, was described from 1976 to 1986. The population fluctuated at high abundance, except for a decline in 1981−1982 following an epizootic of canine parvovirus. Sex ratios were even. Population natality was low, as only 39% of females had viable fetuses. Natality of yearlings (1.5−2.0 years) was lower and more variable than among adults (≥2.5 years). Juvenile (0.8 year) females rarely ovulated. A comparison among 33 radiotelemetered females in 1985 indicated that only territorial adults produced viable fetuses. The proportion of juveniles in spring averaged 0.34. Indices of juvenile survival from birth to the following spring varied from 0.09 to 0.73. Annual survival rates of adults (0.64−0.73) were high and constant. The annual population growth rate (spring to spring) was correlated positively with prey abundance in the preceding winter and negatively with coyote abundance at the beginning of each annual period. Although failure to ovulate and juvenile mortality were identified as key factors in annual variation in population loss, variability in natality among yearlings was identified as the demographic variable associated with relative abundance of coyotes and prey. Body condition of coyotes, as indexed by body mass and internal fat, was not poorer during years of low prey abundance. Interactions between social organization and food availability were implicated in regulation of the lightly exploited high-density population.

Résumé : La démographie d'une population peu exploitée de Coyotes (*Canis latrans*) a fait l'objet d'une étude de 1976 à 1986 dans le comté de Webb au Texas; cette population est reconnue pour ses densités élevées dans le passé. La densité de la population est restée élevée, sauf en 1981−1982 où elle a connu un déclin causé par une épizootie du parvovirus canin. Le rapport mâles : femelles était égal à 1. Le taux de natalité était faible, puisque seulement 39% des femelles portaient des foetus viables; ce taux était plus faible et plus variable chez les jeunes femelles (1,5−2,0 ans) que chez les femelles adultes (≥2,5 ans). L'ovulation était rare chez les femelles juvéniles (0,8 an). Trente-trois femelles ont été suivies par radiotélémétrie en 1985 et les résultats de cette étude ont démontré que seules les femelles adultes territoriales ont produit des foetus viables. La proportion de juvéniles au printemps a été évaluée à 0,34 en moyenne. Les coefficients de survie des jeunes de la naissance au printemps suivant ont été estimés à 0,09−0,73. Les taux annuels de survie des adultes (0,64−0,73) sont restés élevés et constants. Le taux annuel de croissance de la population (printemps au printemps) était en corrélation positive avec l'abondance des proies au cours de l'hiver précédent et en corrélation négative avec l'abondance des coyotes au début de chaque année. Bien que l'échec de l'ovulation et la mortalité chez les juvéniles aient été identifiés comme des facteurs importants de la variation annuelle des pertes au sein de la population, la variabilité de la natalité chez les jeunes a été reconnue comme la principale variable démographique reliée à l'abondance relative des coyotes et des proies. La condition physique des coyotes, évaluée d'après la masse totale et la quantité des graisses internes, n'était pas moins bonne au cours des années où l'abondance des proies s'est avérée faible. La démographie de cette population peu exploitée et de densité élevée est fonction des interactions entre l'organisation sociale et la disponibilité de la nourriture.
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Introduction

In a synopsis of population regulation in coyotes (*Canis latrans*), Knowlton and Stoddart (1983) postulated that densities are determined by the combined effect of food

availability and social intolerance. In the absence of comparable data for food resources, they interpreted a trend toward greater coyote abundance at lower latitudes as evidence for greater food availability in southern regions during the critical winter period. In North America, the greatest abundance of coyotes consistently occurs in the southern region of Texas (Knowlton 1972; Bean 1981; Andelt 1985). The high-density coyote population studied by Andelt (1985) in southern Texas (28°7′N, 97°24′W) exhibited a high degree of sociality, which he viewed as a function of habitat saturation and light human exploitation. The food base for

coyotes in southern Texas is diverse, abundant, and relatively stable. Although about half their diet is fruit and insects in the warm season, coyotes there are restricted to mammalian prey during the cool season (Knowlton 1964; Brown 1977; Andelt et al. 1987; Windberg and Mitchell 1990).

Human-related factors have been identified as a major cause of mortality in several coyote populations (Davison 1980; Tzilkowski 1980; Windberg et al. 1985). The proportion of annual mortality of coyotes attributable to humans appeared to be less in southern Texas (≥ 0.38 (Andelt 1985); 0.57 (Windberg et al. 1985)) than in other regions (0.78 − 1.00) (Knudsen 1976; Davison 1980; Tzilkowski 1980; Pyrah 1984; Crabtree 1988; Gese et al. 1989).

I estimated demographic variables of coyotes annually, along with abundance of mammalian prey in winter, on a study area in southern Texas for 11 years. My objectives were to describe the dynamics of a lightly exploited high-density population (2.0/km^2; Windberg and Knowlton 1988) of coyotes and to evaluate the effects of prey and coyote abundance on coyote population trend, reproduction, and survival of adults and juveniles.

Methods

Abundance of coyotes and prey was estimated annually on a study area of approximately 700 km^2 located 5−40 km northeast of Laredo, Webb County, Texas (27°40'N, 99°20'W), from 1976 to 1986. Reproductive variables, and age and sex composition, were estimated from coyotes trapped on 15 privately owned sites (30−90 km^2 each and 8 km apart) within a larger area (6000 km^2) surrounding the survey area. A different site was intensively trapped each spring (March−April) and fall (October−November), but none of the 15 sites was retrapped within 4 years. Two additional sites (52 and 55 km^2) located 30 and 60 km northwest of Laredo, respectively, were used to study reproduction in relation to the age and territorial classification of females during 1984−1985 (Windberg and Knowlton 1988). Habitats on all study sites were generally similar and representative of the South Texas Plains vegetational area (Gould 1975). Topography, soils, vegetation, climate, and land use for the study area were described by Windberg et al. (1985).

Relative abundance of coyotes in spring (11 May − 21 June) was estimated by the scent-station method (Roughton and Sweeny 1982). Thirty-six 10-station transects were operated during 1980−1986. Linear regression was used to compute comparable indices for 1976−1979, when only 16 transects were operated. Based on 8 field trials, Knowlton and Stoddart (1984) reported coyote visitation rates to scent stations were correlated ($r^2 = 0.79$) with coyote density estimates derived from radioactive feces tagging experiments with radiotelemetered coyotes on sites in Utah and Idaho.

The coyote population was sampled by intensive trapping for 10−40 days on each site. Coyotes were captured with foothold traps using a variety of olfactory attractants (Windberg and Knowlton 1990). After 1980, tranquilizer tabs (Balser 1965) containing 500 mg of propiopromazine hydrochloride (Diamond Laboratories, Des Moines, Iowa) were affixed to traps to reduce injury and trauma. Trapped coyotes were euthanatized by gunshot <24 h after capture.

For each coyote, body mass and length were recorded, the quantity of intraperitoneal fat was rated visually (Windberg et al. 1991), canine teeth and female reproductive organs were preserved, and whole blood was collected for serological tests (Thomas et al. 1984; Guo et al. 1986; Burgess and Windberg 1989). The number of coyotes removed from the study area averaged <1% of the estimated population annually.

Age of coyotes was estimated from the relative size of the pulp cavity, as determined from radiographs (F.F. Knowlton and S.L. Whittemore, unpublished data), and enumeration of cementum layers in microscopic sections of canine teeth (Linhart and Knowlton 1967) prepared by Matson's Laboratory (Milltown, Mont.). Age-classes used for analyses of reproductive variables and body condition were juvenile (0.5 − 1.0 year), yearling (1.5 − 2.0 years), and adult (≥ 2.5 years).

Uteri (fresh or previously frozen) were examined macroscopically to count viable fetuses, resorption sites, or placental scars. Conception dates were estimated from measurement of the crown − rump length of fetuses (Kennelly et al. 1977). Ovaries of coyotes collected in spring were preserved in formalin and examined macroscopically to count luteal glands for estimates of ovulation rates. Ovaries collected in fall were similarly examined for the presence or absence of luteal glands from the preceding spring.

To describe reproductive variables in relation to age and territorial classification, females captured from February 1984 to March 1985 were collared with radiotelemetry transmitters (Windberg and Knowlton 1988). Their subsequent locations were monitored to determine territorial status from breeding to parturition (20 February − 4 May 1985) (Windberg and Knowlton 1988). The marked females were recovered in June 1985 and their reproductive organs examined.

Relative abundance of lagomorphs and rodents was estimated as described by Windberg and Mitchell (1990). For this study, I calculated a composite index of prey abundance in winter (January − February), which I assumed to be the critical period of food limitation for coyotes. Winter diets of coyotes included similar percentages of lagomorphs ($\bar{x} = 43\%$) and rodents ($\bar{x} = 36\%$) over an 8-year period (1979−1986) (Windberg and Mitchell 1990), which suggested that their respective availability as prey was approximately equal. Annual indices of lagomorph and rodent abundance were correlated ($r = 0.69$, $P = 0.02$) during this 11-year study, therefore I adjusted the numerical units of the indices of lagomorph and rodent abundance so that their relative contribution to the composite index of prey abundance was approximately equal. Specifically, a composite index of relative mass (number captured per 1000 trap-nights multiplied by mean mass) for the 7 species of rodents was multiplied by 0.60 and added to the lagomorph index (number/ km^2). White-tailed deer (*Odocoileus virginianus*) and other prey were minor components and relatively constant in coyote diets among years, except for 1980−1981, where I increased the prey index by a coefficient of 1.11 to account for the greater consumption of deer documented during that winter (Windberg and Mitchell 1990).

The scent-station index of coyote abundance (proportion of stations visited × 1000) was the mean for the number of 10-station transects sampled (Roughton and Sweeny 1982). The indices were normally distributed and, therefore, ana-

lyzed by ANOVA. Annual finite rates of population growth (λ) were derived by dividing each index of coyote abundance in the initial spring into the index for the following spring. Annual exponential rates of growth ($\bar{r}$) were then ln λ. Sex and age distributions were analyzed with χ^2 contingency tables.

Data from spring (60%) and fall (40%) were combined to provide annual estimates of the proportion of females ovulating and with fetuses, because differences were not detected between seasons for either variable ($P = 0.19$ and 0.09, respectively). However, only data from spring were used for estimating numbers of ova, implantation sites, and fetuses and resorption of litters, because the accuracy of enumerating those variables in fall was questionable. Females with advanced sarcoptic mange ($n = 28$) were excluded from analyses because this disease decreased natality (Pence and Windberg 1994). An annual index of population natality, which represented an estimate of the number of offspring per adult and yearling female (combined), was derived by multiplying the mean number of fetuses by the proportion of females with fetuses.

The proportions of adults and yearlings that ovulated and produced fetuses were compared by weighted least squares (Grizzle et al. 1969). Mean numbers of ova and fetuses were compared between age-classes and among years by two-factor ANOVA using the general linear model procedure (SAS Institute Inc. 1985); Duncan's multiple-range tests were used to identify significant differences among means. Mean conception dates were compared by t tests. For comparisons between age and territorial classes of females, the proportions with ova and fetuses were analyzed by χ^2 contingency tables and Fisher's exact tests, respectively; mean numbers of ova and fetuses were analyzed by t tests.

Annual survival rates of adult coyotes were estimated from the age distribution by the Chapman–Robson model (Seber 1973). Based on previous survival analyses of this population (Windberg et al. 1985), I truncated the yearling class and combined the older age-classes (≥ 6 years) to fit the model. I believe that the assumptions of a stable age distribution and stationary population required by this estimator of adult survival were generally satisfied because the greatest variations in the age distribution involved differences in annual recruitment. Annual survival rates of adults also were estimated by the product-limit method on adjacent study areas in 1976–1977 and 1979–1980 (Windberg et al. 1985) and for 14 telemetered adult (≥ 3 years) females in 1984–1985 (Windberg and Knowlton 1988). Survival rates for adult age-classes were compared by χ^2 tests (Seber 1973). Annual indices of survival of juveniles from birth to the following spring were derived by dividing the number of juveniles by the number of adult and yearling females at birth, based on reproductive estimates, into the number of juveniles divided by the number of adult females (≥ 3 years) trapped in the subsequent spring. This index incorporated a correction for estimated adult mortality during the interval.

Key-factor analysis is useful to identify mortalities within the life stages that are responsible for population fluctuations over a series of generations (Varley and Gradwell 1960) because population losses are expressed in an additive manner and, thus, are directly comparable. Annual k values were calculated for reproductive losses and losses of juveniles

and adults, using an initial hypothetical maximum number of offspring based on an ovulation rate of 1.0 and the greatest mean number of ova per adult female (7.6) recorded during the study. Annual mortality (K) was the sum of the following submortalities: k_{ova}, which is loss due to failure to ovulate; k_{imp}, which is loss due to failure to implant embryos; k_{rsp}, which is loss due to resorption of fetuses; k_{juv}, which is loss of juveniles from birth to following spring; and k_{ad}, which is annual (spring to spring) loss of adults (≥ 3 years). In addition to graphical comparison, key factors were ranked by the regression coefficient (slope) of each submortality regressed on K (independent variable) (Podoler and Rogers 1975). Linear regression was used to test for relationships between k values and coyote abundance.

Both simple and multiple linear regression were used to analyze relationships between prey and coyote abundance and population growth ($\bar{r}$), survival, and reproductive variables. The combined effect of prey and coyote abundance on coyote natality was analyzed further by partitioning annual estimates into 3 classes of relative abundance for comparing the mean proportions and numbers of ova and fetuses produced by adult and yearling females, respectively, using ANOVA.

Relationships between indices of prey abundance and mean body mass of coyotes in spring were analyzed by linear regression. Mean body masses during years of high versus low prey abundance were compared for adult males, juvenile males, and juvenile females by ANOVA. Yearling males were excluded because of insufficient data in some years; adult and yearling females were excluded because their mass was potentially affected by pregnancy and lactation. Indices of intraperitoneal fat for adult male and juvenile (sexes combined) coyotes in years of high versus low prey abundance were categorical variables analyzed by χ^2 contingency tables. Mean body mass of yearling females in spring in relation to reproductive status (excluding females in the latter half of gestation, because of variable fetal mass) was analyzed by ANOVA. Statistical significance was inferred at $P < 0.05$.

Results

Population abundance and composition

No differences ($P = 0.08$) in relative abundance of coyotes in spring were detected during the first 5 years (1976–1980) (Table 1). Indices of abundance decreased ($P < 0.001$) from 1980 to 1981 and remained low the following year, increased ($P < 0.01$) from 1982 to 1983, and fluctuated ($P = 0.04$) at high levels for the last 4 years of study (1983–1986). Overall, the population neither increased nor decreased significantly for more than 2 consecutive years.

Sex ratios of trapped coyotes did not differ among years ($P = 0.35–0.87$), hence annual samples were combined for seasonal comparisons within age-classes. Males composed 0.52 of captures of adults in both fall ($n = 266$) and spring ($n = 303$). Males composed 0.46 of yearlings captured in both fall ($n = 72$) and spring ($n = 158$) and 0.45 of 194 juveniles in fall and 0.43 of 240 in spring. Neither the adult, yearling, nor juvenile classes differed ($P = 0.10–0.80$) from an even sex ratio. The sex ratios of fetuses did not differ ($P = 0.26$) among years, and the composite (1976–

Table 1. Annual coyote demographic variables and indices of prey abundance in Webb County, Texas, 1976–1986.

Annual period (spring–spring)	Index of prey abundance in preceding winter	Index of coyote abundance in spring (mean ± SE)	Index of natality	Index of proportion of juveniles surviving from birth to spring	Annual survival rate of adults[a]	Annual exponential growth rate ($\bar{r}$)
1976–1977	103	262±23	2.8	0.34	0.71	−0.37
1977–1978	82	181±24	3.9	0.73	0.70	−0.14
1978–1979	139	157±28	3.3	0.58	0.73	0.12
1979–1980	190	177±27	4.0	0.42	0.67	0.34
1980–1981	218	248±26	2.6	0.09[b]	0.67	−0.70
1981–1982	199	123±18	3.8	0.33	0.72	0.27
1982–1983	240	161±26	3.8	0.37	0.64	0.49
1983–1984	164	262±25	2.7	0.32	0.70	0.31
1984–1985	96	358±26	1.3	0.34	0.71	−0.35
1985–1986	84	253±29	2.2	0.50	0.69	0.16
1986	91	295±36	4.7	0.56	0.70	
Mean	146	225	3.2	0.42	0.69	0.13

Note: See Methods for a description of the computation of estimates.
[a]Range of SE = 0.03–0.05.
[b]The low survival of juveniles is attributable to canine parvovirus.

Table 2. Annual age distribution of coyotes ($n = 1230$) captured during fall (October–November) and spring (March–April) in Webb County, Texas, 1976–1986.

Annual period	n	Percentage of coyotes											
		1 yr	2 yrs	3 yrs	4 yrs	5 yrs	6 yrs	7 yrs	8 yrs	9 yrs	10 yrs	11 yrs	12 yrs
1975–1976[a]	38	16	32	26	5	3	11	5	0	0	0	3	0
1976–1977[a]	77	36	18	10	12	3	1	7	7	7	0	0	0
1977–1978[b]	105	56	8	8	7	11	4	2	2	1	1	1	1
1978–1979[b]	140	36	18	16	1	3	8	4	2	3	5	1	4
1979–1980[b]	165	45	17	12	10	4	2	2	6	1	1	1	1
1980–1981[b]	94	9	30	18	15	9	4	7	4	1	2	1	0
1981–1982[b]	102	44	7	15	12	5	5	2	2	3	4	2	0
1982–1983[b]	141	38	26	9	10	6	4	4	0	1	1	1	0
1983–1984[b]	116	27	24	15	4	9	5	9	3	0	1	2	2
1984–1985[b]	108	16	19	18	17	6	10	4	5	2	4	1	0
1985–1986[b]	96	40	18	8	9	13	2	5	1	1	2	0	1
1986[c]	48	52	10	17	2	6	4	2	4	0	2	0	0
Mean		34	19	14	9	6	5	4	3	2	2	1	1

[a]Spring sample only.
[b]Composite sample from fall and spring.
[c]Fall sample only.

1986) ratio of 0.57 males ($n = 279$) did not differ ($P = 0.10$) from equality. Although the proportion of juveniles among trapped coyotes varied ($P < 0.001$) from 0.09 to 0.56 among years (Table 2), it did not differ ($P \geq 0.19$) between fall and spring in any annual period. Nine annual comparisons of the population age distribution (1–12 years) between fall and spring samples yielded only one difference (1979–1980; $P = 0.04$). Therefore, seasonal samples were combined for mean annual estimates of the age distribution (Table 2). In 1980–1981, the proportion of juveniles (0.09) was markedly lower ($P < 0.001$) than in the preceding and following years. Numbers of juveniles were also quite low (0.16) in 1975–1976 and 1984–1985, as in 1980–1981 ($P = 0.27$).

Reproduction

During 1976–1986, only 10 of 186 (0.05) juvenile females ovulated, and only 4 of the 10 had fetuses. Hence, the contribution of juveniles to population natality was inconsequential and is disregarded hereafter. A greater proportion of adults than yearlings ovulated ($P < 0.001$) and had fetuses ($P < 0.001$) (Table 3). Also, mean numbers of ova ($P < 0.001$) and fetuses ($P < 0.01$) were greater among adults than yearlings. Age-specific reproductive data were, therefore, analyzed separately.

During the 11 years of study, dates of conception ranged from 25 January to 14 March. Overall, mean annual dates of conception were 17 February for adults ($n = 60$) and 25 February for yearlings ($n = 20$) ($P < 0.01$). Among

Table 3. Values for annual reproductive variables for adult and yearling coyotes in Webb County, Texas, 1976–1986.

| | Adults | | | | | | | Yearlings | | | | |
Year	Proportion with ova[a]	Proportion with fetuses[a]	n	Mean no. of ova[b]	n	Mean no. of fetuses[b]	n	Proportion with ova[a]	Proportion with fetuses[a]	n	Mean no. of ova[b]	n
1976	0.92	0.81	14[c]	5.3	13	4.2	12	0.62	0.62	8[c]	3.4	5
1977	1.00	0.81	16	6.5	13	5.9	12	0.50	0.30	10	5.5	4
1978	0.95	0.70	20	6.0	9	5.4	7	0.38	0.13	8		
1979	0.93	0.68	28	7.6	11	6.3	10	0.70	0.60	10	5.5	4
1980	0.95	0.55	20	5.8	9	5.8	6	0.43	0.21	14	4.8	4
1981	0.85	0.60	20	6.5	12	7.0	8	0.75	0.75	4	5.3	3
1982	1.00	0.69	13	6.3	4	5.3	3	1.00	1.00	5	6.0	3
1983	0.95	0.63	19	6.1	12	6.1	7	0.76	0.32	19	4.6	9
1984	0.81	0.38	26	4.1	13	4.4	5	0.64	0.14	14	3.4	8
1985	0.92	0.48	25	5.9	16	5.4	10	0.56	0.11	9	4.8	4
1986	0.94	0.81	16	6.9	10	7.3	8	1.00	0.40	5	3.3	3
Mean	0.93	0.65	217	6.1	122	5.7	88	0.67	0.42	106	4.7	47

[a]Composite data for samples in spring and fall of each year.

[b]Data for spring only, and from only those females that had ova or fetuses.

[c]Data for spring only, which were adjusted for average variation between seasonal samples for other years.

adults, 83% of conceptions occurred during 7–26 February, and 65% of yearlings conceived during that period ($P = 0.09$). The remainder of the yearlings conceived later, whereas equal proportions of adults conceived both earlier and later.

A high proportion (0.81–1.00, $\bar{x} = 0.93$) of adult females ovulated annually, but ovulation rates of yearlings ranged from 0.38 to 1.00 ($\bar{x} = 0.67$) (Table 3). Mean numbers of ova per adult female ranged from 5.3 to 7.6 annually, except that there were significantly fewer (Duncan's test, $P < 0.05$) ova (4.1) in 1984, compared with a range of 3.3–6.0 for yearlings. The annual proportion of adults with fetuses ranged from 0.38 to 0.81 ($\bar{x} = 0.65$) ($P = 0.08$); the proportion of yearlings with fetuses varied significantly ($P < 0.01$) among years, from 0.11 to 1.00 ($\bar{x} = 0.42$). The relatively low proportion of adults (0.38) and yearlings (0.14) with fetuses in 1984 was attributable to a greater proportion of both adults (0.58; $n = 12$; $P < 0.001$) and yearlings (0.67; $n = 6$; $P = 0.02$) that resorbed their entire litter than in all other years. Mean numbers of fetuses per adult female ranged from 4.2 to 7.3 ($\bar{x} = 5.7$) during 1976–1986 (Table 3). Among yearlings, data were insufficient for making annual estimates, but the composite (1976–1986) mean number of fetuses was 4.3 ($n = 27$).

Adult females produced 75–96% ($\bar{x} = 85\%$) of the total offspring annually (Fig. 1). Yearlings exhibited greater annual variation than adults in the proportion ovulating (CV = 31 vs. 6%) and the proportion with fetuses (CV = 70 vs. 22%), whereas variation in the mean numbers of ova (CV = 21 vs. 16%) was similar (Table 3).

A composite sample (1976–1986) of adult and yearling females ($n = 334$), aged by means of cementum analysis, revealed few additional age-specific reproductive patterns (Table 4). There were no differences ($P = 0.45$) in the proportion of females with ova from 3 to 10–12 years of age (Table 4). The oldest females (10–12 years) had a lower proportion ($P = 0.04$) of fetuses than younger adult females. The proportion of females that resorbed their entire litter did

not differ ($P = 0.40$) with age. Differences ($P = 0.03$) in mean number of ova among adult females were not reflected in the mean number of fetuses ($P = 0.06$), nor was a significant trend with age discernible for either variable (Table 4).

During spring 1985, territorial classification and reproductive success were determined for 33 females equipped with radiotelemetry transmitters. No juveniles (2 territorial and 3 transient) ovulated. Among yearlings, the 1 territorial female ovulated but did not implant; only 3 of 9 transients ovulated and the 2 that implanted subsequently resorbed all fetuses. All 11 territorial adults and 5 of 7 transient adults ovulated. Mean number of ova did not differ ($P = 0.22$) between territorial (5.5) and transient (4.6) adults. A greater proportion ($P < 0.01$) of territorial (0.91) than transient adults (0.29) implanted. Likewise, a greater proportion ($P = 0.04$) of territorial (0.55) than transient adults (0 of 7) produced viable fetuses. The 3 transient adults that ovulated but failed to implant were 10–12 years old; 2 territorial females with viable fetuses were 8 and 9 years old. The low reproductive success among telemetered females corresponded to the relatively low natality for the population sample in 1985 (Tables 1 and 3).

Among 3 telemetered females that occupied the same territorial range during spring 1985, the juvenile did not ovulate, the 5-year-old resorbed 4 fetuses early in gestation, and had hypotrophied mammae, and the 3-year-old had 3 placental scars and 1 resorption site and had distended mammae and loss of mammary hair as evidence of whelping and nursing. The two adult females had similar body mass (9.5 vs. 10.0 kg) and length (83.2 vs. 78.7 cm) when captured on 12–14 February 1985.

Survival and mortality

Annual survival rates of adults estimated from the age distribution ranged from 0.64 to 0.73 (CV = 4%) during the study (Table 1). Annual survival rates of adults derived by radiotelemetry studies (Windberg et al. 1985; Windberg and Knowlton 1988) were 0.71 (SE = 0.11) in 1976–1977, 0.60

Fig. 1. Natality of the coyote population, and of adult and yearling females, in Webb County, Texas, 1976–1986.
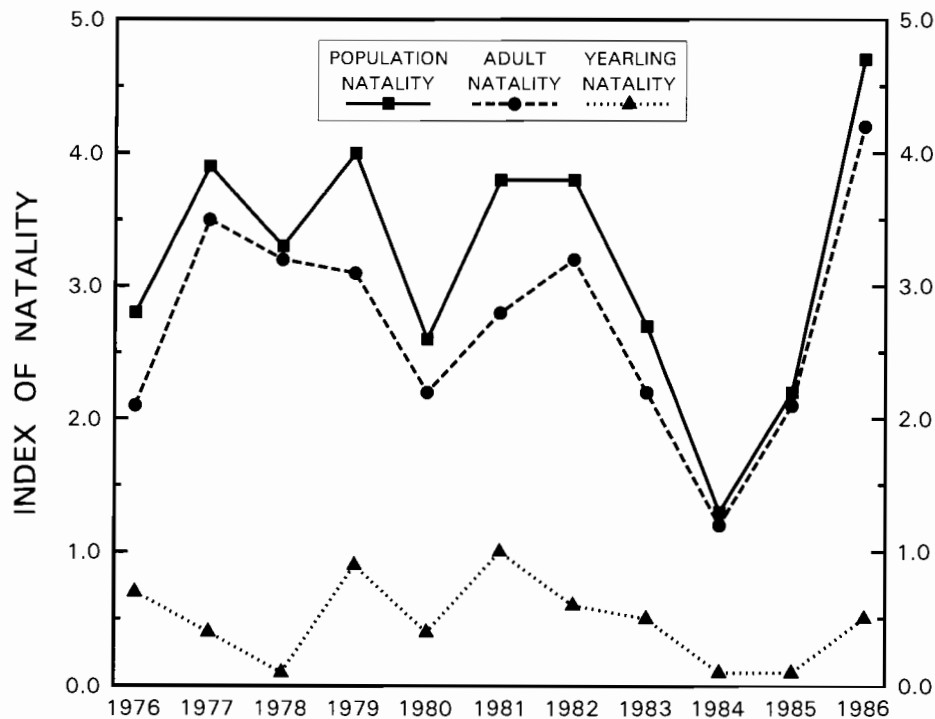
Table 4. Age-specific reproductive variables for the composite sample of yearling and adult females in Webb County, Texas, 1976–1986.

Age (yrs)	Proportion with ova	Proportion with fetuses	Proportion that resorbed entire litter	n	Mean no. of ova[a]	Mean no. of fetuses[a]	n
2	0.63	0.37	0.15	106	4.9	4.3	27
3	0.84	0.57	0.10	68	5.7	5.2	32
4	0.93	0.68	0.08	40	7.0	6.6	17
5	0.96	0.54	0.19	26	6.3	5.3	9
6	0.92	0.67	0.08	24	7.5	6.4	10
7	0.96	0.64	0.24	25	7.4	6.8	10
8	1.00	0.85	0.15	13	6.8	5.2	6
9	1.00	0.67	0.00	15	5.2	4.6	5
10–12	0.88	0.24	0.18	17	6.3	4.0	3

[a]Data are from only those females with both ova and fetuses.

(SE = 0.16) in 1979–1980, and 0.67 (SE = 0.14) in 1984–1985, which are similar to the estimates from the age distribution.

To assess age-specific survival of adults, a composite age distribution of the population from 1976 to 1986 was examined (Table 2, Fig. 2). Although the age distribution differed among years ($P < 0.001$) and the population fluctuated ($P < 0.01$), I assumed that the composite distribution averaged out variations and was representative of the population for the 12-year period. Annual survival from 1 to 2 years of age (0.56) was lower ($P = 0.01$) than among older coyotes (0.69). The pattern of the survivorship curve, based on the logarithm of age-class sizes, indicated constant survival from 2 to 8 years and decreased survival thereafter (Fig. 2). The 2 oldest coyotes captured were 12.5 years.

Annual indices of juvenile survival (birth to the following spring) ranged from 0.32 to 0.73 (CV = 31%), except for 0.09 in 1980–1981 (Table 1). Annual survival estimates for adults and juveniles were not correlated ($r = 0.21$, $P = 0.54$).

Key-factor analysis was used to partition annual population losses. The graphical distribution of k values for reproductive, juvenile, and adult losses during 1976–1986 implicated juvenile mortality (birth to spring) as the key factor (Fig. 3). Comparison of slope coefficients for regression of each submortality on K showed a stronger relationship with k_{juv} ($b = 0.62$) than k_{ova} ($b = 0.19$), k_{imp} ($b = 0.07$), k_{rsp} ($b = 0.10$), or k_{ad} ($b = 0.01$). The high juvenile mortality in 1980 was attributable to a canine parvovirus epizootic (Thomas et al. 1984), which was an atypical form of mortal-

Fig. 2. Survivorship curve for adult coyotes, based on a composite age distribution (●) and logarithms of age-class size (■) in Webb County, Texas, 1976–1986.
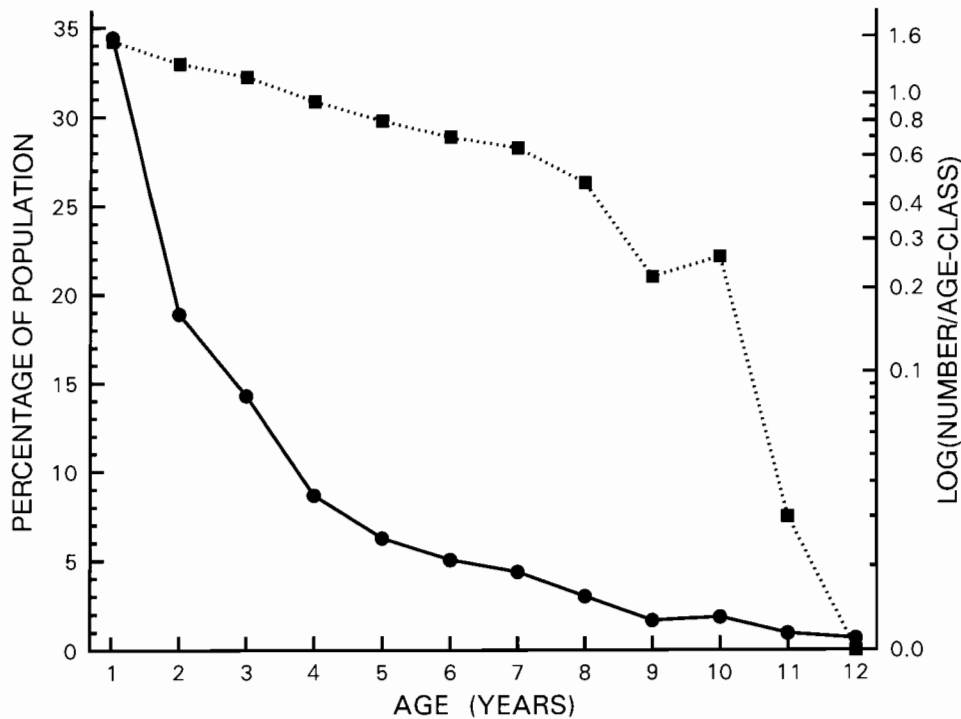
Fig. 3. Graphical key factor analysis of annual losses in coyote population in Webb County, Texas, 1976–1986. Submortalities of K (annual mortality) were k_{ova} (failure to ovulate), k_{imp} (failure to implant embryos), k_{rsp} (resorption of fetuses), k_{juv} (juvenile mortality from birth to spring), and k_{ad} (annual adult mortality).
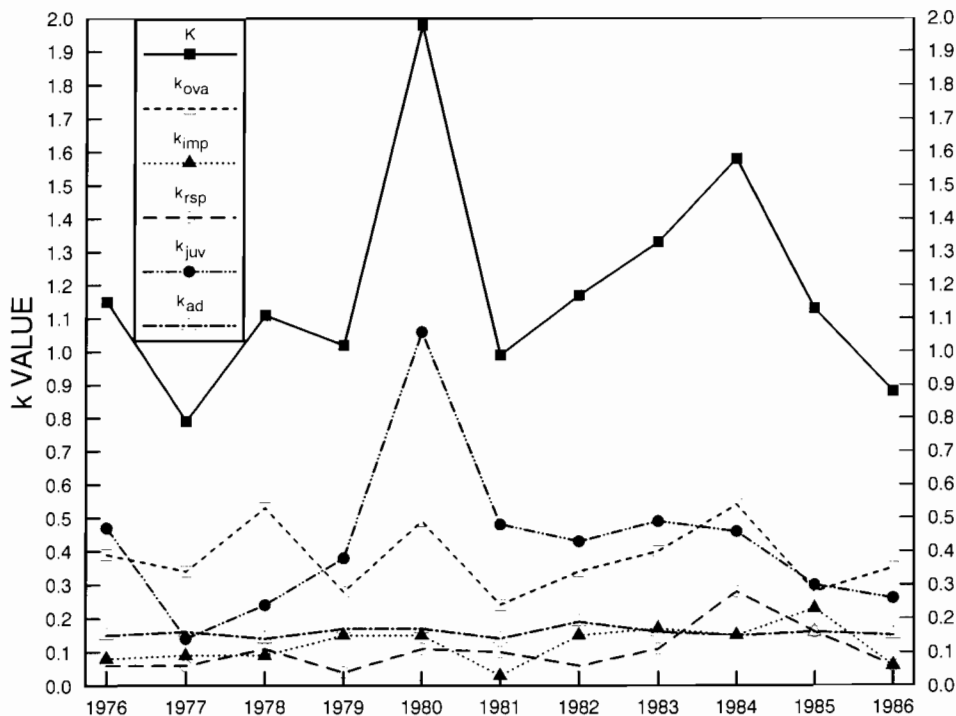
ity during the period of study. Exclusion of 1980 data probably provided a more representative analysis of population losses and yielded similar slope coefficients for k_{juv} ($b = 0.35$) and k_{ova} ($b = 0.27$). Thus, failure to ovulate and birth-to-spring mortality were the key variates of annual population loss. Linear regression of the submortalities (k_{ova}, k_{imp}, k_{rsp}, k_{juv}, k_{ad}) on initial coyote abundance showed no strong relationships ($r^2 = 0.01–0.25$).

Table 5. Coefficients for relationships between prey abundance and coyote abundance with selected demographic variables in Webb County, Texas, 1976–1986.

Demographic variable	Prey abundance			Coyote abundance			Prey and coyote abundance		
	r	df	P	r	df	P	R^2	df	P
Population growth ($\bar{r}$)	0.80	7	**<0.01**	−0.62	7	0.08	0.68	6	**0.01**
Survival of adults	−0.52	7	0.16	0.14	7	0.72	0.30	7	0.17
Survival of juveniles	−0.44	7	0.24	−0.31	7	0.42	0.71	7	**<0.01**
Population natality	0.21	9	0.54	−0.57	9	0.07	0.33	7	0.11
Natality of adults	0.01	9	0.98	−0.37	9	0.26	0.19	8	0.21
Proportion with ova	−0.24	9	0.48	−0.39	9	0.24	0.15	8	0.68
Proportion with fetuses	−0.09	9	0.79	−0.36	9	0.28	0.24	8	0.51
Mean no. of ova	0.31	9	0.35	−0.61	9	0.05	0.38	8	0.06
Mean no. of fetuses	0.22	9	0.51	−0.34	9	0.31	0.12	8	0.74
Natality of yearlings	0.70	8	**0.03**	−0.76	8	**0.01**	0.68	7	**<0.01**
Proportion with ova	0.22	9	0.51	0.06	9	0.86	0.09	8	0.80
Proportion with fetuses	0.58	9	0.07	−0.50	9	0.12	0.39	8	0.06
Mean no. of ova	0.61	8	0.06	−0.85	8	**0.01**	0.75	7	**<0.01**

Note: Statistical significance is to be inferred for *P* values in boldface type.

Analysis of demographic factors

To validate the demographic estimates (Table 1), a rate of population growth ($\lambda = 1.13$, $\bar{r} = 0.12$) was calculated from the overall mean estimates for 1976–1986 as follows:

(initial population (1.0) × proportion of females (0.5)

× (natality index (3.2) × proportion of adult and

yearling females (0.66)) × survival of juveniles

(birth to spring) (0.42) + (initial population (1.0)

× annual survival of adults (0.69))

The $\bar{r}$ value (0.12) from this computation compared favorably with the overall $\bar{r}$ value (0.13) from 1976–1986, derived from indices of coyote abundance (Table 1), which suggested that estimates of demographic variables and population abundance were in accordance.

Annual indices of prey abundance in winter varied 3-fold (CV = 40%) during the 11 years (Table 1). A marked decline in prey abundance occurred from 1982 to 1985, when total rainfall during March–October (an index of forage production during growing season) averaged half (26.2 cm) of mean rainfall (50.9 cm) for the other 8 years (National Oceanic and Atmospheric Administration 1976–1986). Overall, however, prey abundance and rainfall patterns were unrelated because March–October rainfall varied little (37.6–38.6 cm) during 1977–1979, when prey indices trended upward, whereas rainfall varied 3-fold (25.9–93.2 cm) during 4 years (1979–1982) of stationary (CV = 10%) and high prey abundance (Table 1).

The coyote population decline during 1980–1981 resulted from extreme loss of juveniles (Table 1) caused by canine parvovirus. Because that mortality factor was significant in only 1 year of the study, I excluded the 1980–1981 data from the following analyses of demographic relationships involving survival. I assumed, however, that canine parvovirus had no effect on fecundity (Pollock 1984).

Correlation analysis for 9 annual periods from 1976 to 1986 (excluding 1980–1981) showed a positive relationship

($r^2 = 0.64$) between prey abundance in the preceding winter and annual population growth ($\bar{r}$) (Tables 1 and 5). The combined influence of prey abundance in winter (positive) and coyote abundance at the beginning of each annual period (negative) on $\bar{r}$ ($R^2 = 0.68$) was significant ($P = 0.01$) (Table 5).

To identify specific demographic variables associated with the influence of prey and coyote abundance on population growth, I regressed estimates of survival and natality on the indices of abundance (Table 5). There was no relationship between survival of adults and abundance of prey or coyotes. A correlation ($P < 0.01$) for the combined effect of prey and coyote abundance on survival of juveniles may be of questionable biological significance because there were no individual correlations with prey or coyote abundance (Table 5). Indices of survival of juveniles were not correlated ($r = 0.40$, $P = 0.23$) with indices of natality.

Relationships between population natality and prey and coyote abundance, individually and collectively, were insignificant (Table 5). Because natality differed between adults and yearlings (Tables 3 and 4), the influence of prey and coyote abundance on reproductive variables was analyzed within those age-classes (Table 5). Neither adult natality nor any of its components (rates of ovulation and pregnancy, numbers of ova and fetuses) were correlated with prey or coyote abundance. The combined effect of prey (positive) and coyote (negative) abundance on natality of yearlings was the same as for population growth. That relationship evidently involved both the proportion of yearlings with fetuses and their number of ova. Although samples were insufficient for making annual estimates, the number of fetuses probably reflected the number of ova among yearlings because the composite (1976–1986) estimate of the mean number of fetuses (4.3) was only 12% less than that for ova (4.9).

Relationships between reproductive variables for adults and yearlings and abundance of prey and coyotes were examined further by partitioning the indices of abundance into three categories (Table 6). The comparisons revealed a greater proportion ($P = 0.04$) of yearlings with fetuses dur-

Table 6. Annual reproductive variables (unweighted means) for adult and yearling females in relation to relative prey and coyote abundance in Webb County, Texas, 1976–1986.

Index of abundance	No. of years	Adults				Yearlings		
		Proportion with ova	Proportion with fetuses	Mean no. of ova	Mean no. of fetuses	Proportion with ova	Proportion with fetuses	Mean no. of ova
Low prey − high coyote[a]	4	0.89	0.62	5.6	5.3	0.71	0.29	3.7
Intermediate[b]	4	0.96	0.67	6.1	5.8	0.52	0.24	5.0[c]
High prey − low coyote[c]	3	0.93	0.66	6.8	6.2	0.77	0.73	5.6

[a]Ranges were 84–103 for prey and 253–358 for coyotes.
[b]Ranges were 82–218 for prey and 157–262 for coyotes; these specific combinations of prey and coyote indices did not fit other categories.
[c]Data for 3 years only.
[d]Ranges were 190–240 for prey and 123–177 for coyotes.

Table 7. Mean body mass of adult males, juvenile males, and juvenile females in spring during years of high and low prey abundance in Webb County, Texas.

Relative prey abundance	Mean index of prey abundance in winter	Body mass (kg)					
		Adult males		Juvenile males		Juvenile females	
		Mean	n	Mean	n	Mean	n
High[a]	212	10.9	48	9.2	39	8.4	54
Low[b]	91	11.0	72	8.8	29	8.0	51

[a]Data for 4 years (1979–1982).
[b]Data for 5 years (1976–1977 and 1984–1986).

ing years of high prey abundance and low coyote abundance than in other years, and fewer ($P < 0.01$) ova shed by yearlings in years of low prey abundance and high coyote abundance.

Body condition
Because population growth and natality of yearling females were directly associated with relative prey abundance in winter (Table 5), I examined the relationship between mean body mass (an index of body condition) of coyotes in spring and prey abundance in the preceding winter. There were no relationships ($P \geq 0.12$) between mean body mass of adult males ($r = -0.23$), juvenile males ($r = 0.33$), or juvenile females ($r = 0.50$) with prey abundance during the 11 years. I also compared body masses of the same age and sex classes during 4 years (1979–1982) of high prey abundance ($\bar{x}$ index = 212) and 5 years (1976–1977 and 1984–1986) of low prey abundance ($\bar{x}$ index = 91) (Table 7). Mean body mass did not differ among adult ($P = 0.66$) or juvenile males ($P = 0.23$) between years of high and low prey abundance. Mean body mass of juvenile females was greater ($P = 0.04$) during years of high prey abundance than during years of low prey abundance. Additionally, I compared indices of intraperitoneal fat deposits in composite samples from 2 years (1981–1982) of high prey abundance versus 3 years (1984–1986) of low prey abundance. The frequency distribution of fat indices did not differ among either adult males ($P = 0.90$) or juveniles ($P = 0.22$) between years of high and low prey abundance.

Body masses of yearling females in spring (1976–1986) were compared to examine the relationship between body condition and reproductive success. Nonovulating yearlings ($\bar{x} = 8.1$ kg, $n = 23$) were lighter ($P = 0.04$) than yearlings that either ovulated but failed to implant ($\bar{x} = 9.0$ kg, $n = 8$), implanted but resorbed fetuses ($\bar{x} = 8.7$ kg, $n = 12$), or had viable fetuses ($\bar{x} = 8.7$ kg, $n = 12$).

Discussion
Estimates of demographic variables are subject to inherent sampling bias. The most troublesome bias in this study was potential overrepresentation of transients (usually younger individuals) in population samples trapped from small areas because they had larger ranges than territorial coyotes (Windberg and Knowlton 1988, 1990; Stoddart et al. 1989). I found lower natality among juveniles and yearlings than adults, and among transients than territorial females. A greater representation of transients in the trapped samples (Windberg and Knowlton 1988) probably resulted in underestimation of population natality. This, coupled with overestimation of the ratio of juvenile to adult females, would cause the index of juvenile survival to be overestimated. Capture procedures used for the radiotelemetry studies of coyote survival (Windberg et al. 1985) were comparable to this study and hence also biased toward transients. Because greater mortality among transients than among territorial coyotes has been recorded (Andelt 1985; Crabtree 1988; Gese et al. 1989), annual survival rates of adults and overwinter survival of juveniles reported for this population by Windberg et al. (1985) were probably underestimated. Nevertheless, I assumed that sampling biases associated with demographic estimates were constant in nature among years because my methods were consistent throughout the study.

Saturated habitat, differences in habitat or food supply, and human exploitation are factors usually associated with

differential emigration of coyotes (Davison 1980; Andelt 1985; Crabtree 1988). I assumed that egress and ingress were equal in the open population because these factors appeared similar throughout my extensive study area.

Demography

Population density averaged 2.0 coyotes/km^2 on two areas in Webb County (15−25 km west of my study area) during spring 1985 (Knowlton et al. 1986; Windberg and Knowlton 1988). The index of abundance for my area in spring 1985 (253) was 12% greater than the overall mean (1976−1986, excluding 1981). Hence, coyote densities varied around 2.0/km^2 in spring throughout this study. In comparison, Andelt (1985) estimated a coyote density of 0.8−0.9/km^2 in spring on the Welder Wildlife Refuge and reported densities ranging from 0.15 to 0.54/km^2 for six other studies. Knowlton (1972) speculated that densities were 1.5−2.3/km^2 in fall throughout southern Texas.

Several studies noted that the proportion of juveniles breeding was low and variable (Gier 1968; Knudsen 1976; Todd and Keith 1983; Jean and Bergeron 1984), but only Knudsen (1976) and Jean and Bergeron (1984) reported lower rates of pregnancy for yearlings (2 years) than for adults. In this study, virtually no juvenile females ovulated, and natality was low and variable among yearlings. Females aged 3−9 years were the primary reproductive cohort, with similar natality among age-classes. The only evidence of reproductive senescence was a lower proportion of 10- to 12-year-old females with fetuses. Clearly, the onset of breeding was deferred and natality suppressed in this coyote population. Based on composite estimates of age distribution and proportion of females with fetuses, only 39% of females produced offspring. An additional 17% of females initiated the reproductive process by ovulating but did not produce viable fetuses.

Overall, mortality in utero was not a significant reproductive loss in this coyote population. However, resorption of entire litters was greatest in 1984, which was the year when a high prevalence of antibodies against Lyme disease (*Borrelia burgdorferi*) first occurred in the population (Burgess and Windberg 1989). An association between Lyme disease and the number of resorptions was reported in dogs (*Canis lupus*) (Gustafson et al. 1993) and hence may have contributed to greater resorption among coyotes.

The relatively low proportion of juveniles in this coyote population compared with others (Knowlton 1972; Davison 1980; Todd et al. 1981) resulted partly from suppressed natality. The composite index (1976−1986) of juvenile survival, the other component of recruitment, from birth to spring was 0.42. Although the index may have been inflated because of sampling biases identified above, the bias was not great because the overall proportion of juveniles in spring was similar to the overall annual proportion of mortality of adults (0.34 vs. 0.31) in the relatively stationary population.

A high loss of juveniles in 1980 was attributable to a canine parvovirus epizootic (Thomas et al. 1984). The disease causes high mortality of juvenile canids (Pollock 1984). The epizootic began between April and November 1980 (Thomas et al. 1984) in the naive population, thereby exposing vulnerable juveniles to infection. A high prevalence of neutralizing antibodies against parvovirus among adult coyotes (Thomas et al. 1984) and transfer of maternal antibodies to offspring (Pollock 1984) undoubtedly reduced the susceptibility of juveniles to the disease in subsequent years.

The causes of mortality among juvenile coyotes, particularly during their early life, are largely unknown. Hookworm (*Ancylostoma caninum*) parasitism has been implicated as a potential factor in losses of juveniles in southern Texas (Mitchell and Beasom 1974; Pence and Windberg 1984; Andelt 1985). Canine distemper was endemic in this population (Guo et al. 1986), and thus a potential cause of juvenile mortality (Pence and Custer 1981). A sarcoptic mange epizootic occurred during this study, but a high rate of mortality among mange-infected coyotes was judged to be compensatory with overall population mortality (Pence and Windberg 1994). Four cases of maternal cannibalism of neonates, immediately post partum, were observed among 14 primiparous captive females maintained on subnormal diets during gestation (Sayles 1984), but this has not been documented in wild coyotes. In two cases, Camenzind (1978) suspected infanticide by neighboring territorial coyotes at dens in northwestern Wyoming. McLeod (1990) suggested that the killing by dominant females of juveniles born to subordinates may be common in wolves (*C. lupus*). In summary, other studies suggest that diseases and infanticide may contribute to loss of juveniles, but their significance in wild populations is unknown.

Annual survival of adult coyotes was remarkably constant throughout this and a related study (Windberg et al. 1985). My estimate of mean annual adult survival (0.69) was similar to the rate of 0.68 reported by Andelt (1985) in southern Texas, and in the middle of the range of estimates reported for southeastern Washington (0.90) (Crabtree 1988), southeastern Colorado (0.87) (Gese et al. 1989), northern Utah (0.47), and southern Idaho (0.51) (Davison 1980). The population age structure depicted a Type I survivorship curve, with high survival early in life followed by higher mortality among older individuals.

Population regulation

The coyote population that I studied exhibited adjustments to stationary high densities. A density-dependent population response followed perturbation by the parvovirus epizootic. Indices of coyote abundance in spring ranged from 248 to 358 during 6 of 11 years. That level of abundance apparently represented an upper limit for the population. Similarly, mean indices of coyote abundance from 11 scent-station surveys conducted annually in fall (September) throughout the southern region of Texas during 1972−1981 ranged from 281 to 391 (Bean 1981; J.R. Bean, unpublished data).

Scarcity of prey over winter decreased reproduction and depleted fat deposits of coyotes in Alberta (Todd and Keith 1983). There was no evidence that either natality or body condition of adult coyotes was adversely affected by the lowest levels of prey abundance observed during this study. The positive effect of greater prey abundance on coyote population growth appeared to be constrained by the negative effect of higher coyote density. Food limitation per se apparently never depressed population density because equally high levels of coyote abundance occurred when prey abundance was highest and lowest.

Watson and Moss (1970) listed 4 conditions for evaluating the concept that behavioral factors limit a population by means of socially induced mortality or suppression of recruit-

ment. As summarized by Flowerdew (1987), these are as follows: (1) a substantial part of the population does not breed; (2) nonbreeders are physiologically capable of breeding in the absence of breeders; (3) the population does not completely use an essential resource; and (4) the effect of socially induced mortality, or suppressed recruitment, decreases after substantial losses from other causes. If the listed conditions are met and population growth varies with availability of food, then food and behavior are both limiting factors (Flowerdew 1987).

I assessed these 4 conditions for the coyote population studied in southern Texas. First, reproductive output was clearly suppressed because, overall, only 39% of females reproduced annually. Second, although I did not determine the capability of nonbreeding females to reproduce in the absence of breeders, reproduction by juvenile females has been observed in other populations (Gier 1968; Knudsen 1976; Todd and Keith 1983; Jean and Bergeron 1984), and a relatively high proportion of yearlings had fetuses during 1981 and 1982, when coyote abundance was low. Because yearling females that failed to ovulate had less body mass than yearlings that ovulated, smaller yearlings may not have been physiologically able to reproduce. Of course, the smaller size of some individuals may have resulted from retarded growth due to prolonged behavioral subordination. Third, the upper level of coyote abundance occurred at both high and low prey abundance. An absence of measurable changes in body condition of coyotes indicated that food resources were never reduced to levels at which the condition of individuals was adversely affected. Further, no differences in body condition were detected between 26 territorial and 33 transient females during low prey abundance in 1985 (Windberg et al. 1991), which suggested that social status did not significantly affect access to food. Fourth, greater natality of yearlings during years of high prey abundance and low coyote abundance is interpreted as a compensatory response to the usual constraint of those factors. I infer that social behavior was an important influence on the regulation of this coyote population, because the conditions proposed by Watson and Moss (1970) appear to be applicable.

Interrelationships between social behavior and variation in food supply as mechanisms of population regulation were described for wolves (Packard and Mech 1980) and red foxes (*Vulpes vulpes*) (Lindström 1989). In the coyote population I studied, social behavior apparently influenced rates of increase through variation in reproduction, particularly among yearling females. Andelt (1985) found only one litter per social group in southern Texas, and only territorial adult females produced viable fetuses during my radiotelemetry study in 1985. Windberg and Knowlton (1988) found that a high proportion of yearlings (0.44) were transients in this population, and no telemetered transients (adult or yearling) had viable fetuses in 1985. Thus, I infer that suppression of reproduction among yearlings was behaviorally induced, either directly by sexual competition within territorial social groups, as in wolves (Packard et al. 1985), or by relegation to transient (nonterritorial) status. Also, one-third of adults failed to produce viable fetuses each year, which I suspect was due to the same behavioral constraints as those implicated for yearlings. Most barren adults (0.78), especially senescent females, experienced disruption of reproduction,

either by failure to implant fetuses or by resorption. Such disruption may have resulted from behavioral antagonism, as in the cases described by Knowlton and Stoddart (1983) among captive coyotes, where resorption of fetuses occurred among subordinates that were harassed by dominant females. Studies with captives by Hodges (1990) demonstrated an alteration of reproductive hormones associated with behavioral subordination that resulted in loss of fecundity among mature females. I believe that social behavior was the proximate cause of reproductive suppression, but the specific mechanisms responsible for annual variations in population natality are unclear. Behavioral reproductive suppression likely occurred among both transients and subordinate females in territorial groups in this high-density population. Any reduction in the proportion of transients associated with lower coyote abundance may result in measurably greater natality among yearlings. A combination of low coyote abundance and high prey abundance may have influenced behavior and allowed reproduction by some subordinate females in territorial groups. Cases of two litters per den reported elsewhere (Nellis and Keith 1976; Andrews and Boggess 1978; Camenzind 1978) provide circumstantial evidence of reproduction by more than one female per social group of coyotes. In wolves, the frequency of multiple litters per pack ranged from 7% (Ballard et al. 1987) to 41% (Harrington et al. 1982). Because multiple litters were not observed in unexploited wolf populations that were either saturated or increasing, Ballard et al. (1987) suggested that they may represent a form of compensation for human exploitation. The mechanism involved there was likely removal of dominant individuals, which resulted in multiple matings among subordinates (Packard et al. 1985).

Another potential component of socially induced mortality in this population may be over-winter losses of juveniles. Apparent differential age biases in seasonal samples of the population precluded estimation of mortality of juveniles from fall to spring during my study. A previous 4-year study (Windberg et al. 1985) showed relatively high over-winter mortality of juveniles. Dispersal of juveniles usually occurs during fall and winter (Davison 1980; Crabtree 1988; Gese et al. 1989). Most juveniles that disperse probably become transients for some time (Crabtree 1988), and higher rates of mortality ($1.4\times - 2.8\times$) were reported for transients than for territorial coyotes (Andelt 1985; Crabtree 1988; Gese et al. 1989). Although normally low in southern Texas (Andelt 1985), the proportion of juveniles that disperse from territorial groups may vary with coyote or prey abundance. Hence, social factors may affect over-winter juvenile mortality in this coyote population. Zimen (1976) found that greater oppression of subordinates among captive wolves was associated with availability of less food, and postulated that dispersal may be directly related to food deficiency. Annual variation in over-winter juvenile mortality may be related to the proportion of transients in the population, likely a sequential function of intensity of social interactions, population density, and ultimately food availability. Moehlman (1987), for example, observed that some juvenile golden jackals (*Canis aureus*) left their natal ranges during seasonal food scarcity and returned 4−5 months later, when food became abundant.

I infer that the coyote population in southern Texas was

regulated at a high equilibrium density. Regulation of the population was demonstrated by its rapid growth to previous high densities (Murdoch 1970) after a significant reduction by the parvovirus epizootic. As in wolves (Packard and Mech 1980; Keith 1983), the social organization of coyote populations appears to interact with food availability to stabilize numerical fluctuation (Knowlton and Stoddart 1983). At saturation density, social factors appear to severely restrain recruitment.

Human exploitation (reduction) of coyote populations potentially releases internal social constraints that could stimulate compensatory growth toward previous densities, within the limits of food availability. Of course, reduction in coyote abundance may result in a greater amount of available food per coyote. The demographic response of coyote populations to lower densities and associated greater availability of food should be a reversal of the sequence described by Eberhardt (1977). In general terms, that means (i) greater survival of juveniles, (ii) greater reproduction by young individuals, (iii) greater natality in the population, and (iv) greater survival of adults. Accordingly, Davison (1980) documented greater recruitment of juveniles in a heavily exploited than in a lightly exploited population, and Knowlton (1972) reported larger litters in areas of most intensive removal of coyotes.

The resilience of coyote populations to increased mortality via compensatory demographic responses hinders management schemes based on the principle of population reduction by indiscriminate removal of coyotes. Alternatively, the demographic effect of disruption of the coyote social organization by selective removal of various proportions of behaviorally dominant individuals may warrant investigation. At present, the greatest potential for effective long-term management of coyote populations may lie in the inhibition of reproduction, because that could eliminate the primary mechanism of demographic response without disrupting the social organization.

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